

8. Predicting locations of Asiatic houbara (*Chlamydotis [undulata] macqueenii*) leks: Do males congregate at hotspots?

Abstract

Leks are sites at which males cluster to mate with females. Formation of leks is predicted to occur at hotspots, i.e., sites of high female utilisation, because these are the sites where males will most likely encounter females. Here, I test three specific predictions of the hotspot model of lek formation, for a population of Asiatic houbara in west central Saudi Arabia. I examined whether houbara males locate display sites where (1) females spend the most time, (2) females occur in the highest numbers or (3) most female home ranges overlap. Two of the three hotspot model predictions were supported. Display sites of houbara were more likely to be found where female numbers were high, and at sites where many female home ranges overlapped, but they did not occur at sites where females spent the most time. I suggest this strategy best suits the environmental conditions faced by desert species such as houbara, because food is patchily distributed and female movements are unpredictable at a local level, but show strong fidelity to general sites. I found no evidence that another male strategy for locating females (becoming a mobile floater) occurred in this population. I discuss the likelihood that alternate models for lek formation (female preference, hotshot) may explain patterns of lek distribution in houbara.

Introduction

Leks are aggregation sites of males, which females visit for the primary purpose of fertilization (Bradbury 1981, Hoglund & Alatalo 1995). Aside from sperm, males at these sites provide nothing else for females, and take no further part in the incubation or rearing of young. Lekking occurs in only a few bird species that belong to many taxonomic groups (Hoglund & Alatalo 1995). The most conspicuous aspect of any lekking species is male aggregations or clusters. Because clusters have a primarily sexual function, understanding why males cluster in the places that they do should allow insights into the process of sexual selection (Hoglund & Alatalo 1995).

Three groups of hypotheses for the formation of leks and the role of male participation are commonly considered (e.g., Hoglund & Alatalo 1995, Hugie & Lank 1997, Westcott 1997). First, because observations suggest that only a few males at leks are responsible for most matings with females (e.g., Hovi *et al.*, 1994), then one strategy for unsuccessful males may be to form a cluster around "hotshot" males that have high success rates and thereby intercept females that are attracted to the successful males ("hotshot" model, Arak 1983, Beehler & Foster 1988, Hoglund & Robertson 1990, Widemo & Owens 1995). Second, clusters form because they are mutually beneficial for males and females. Males cluster at these sites because females prefer to mate with males there ("female preference", "black-hole" models, Bradbury 1981, Gibson *et al.*, 1990, Clutton-Brock *et al.*, 1992). Females may choose to mate with aggregated males for many reasons: because predation risk is reduced (e.g., Gosling 1986), mate search costs are reduced (Alexander 1975), male comparison is possible (Emelen & Oring 1977), or because harassment from other males is reduced (Clutton-Brock *et al.*, 1993). Finally, males cluster at sites where they have a high likelihood of encountering females ("hotspots", Alexander 1975, Bradbury 1981, Bradbury *et al.*, 1986). Hotspots are predicted to occur at sites where female densities are highest (e.g., Bradbury & Gibson 1983, Gosling & Petrie 1990), where female home ranges have the highest level of overlap (e.g., Bradbury *et al.*, 1986), where female movement is greatest (e.g., Westcott 1997), and/or where females spend the most time (e.g., Kruijt *et al.*, 1972). Testing predictions from each of these three groups of hypotheses will help develop a clearer

understanding of how leks function, and in turn, the role of sexual selection in the behaviour of lekking species.

Asiatic houbara (*Chlamydotis [undulata] macqueenii*) in Mahazat as-Sayd Reserve, Saudi Arabia, have dispersed or exploded leks (*sensu* Hoglund & Alatalo 1995; Chapter 7). This is in concordance with anecdotal descriptions of male behaviour for both migratory and resident populations throughout the range of the houbara (Alekseev 1980, Ponamareva 1983, Lavee 1985, 1988, Symens 1988, Launay & Loughland 1995, Launay *et al.*, 1997), and for male behaviour of *C. undulata fuereventura* on the Canary Islands (Collins 1984). Display sites of small scattered groups are located on small rises and open areas (e.g., Collins 1984, Yang *et al.*, 2002), presumably to increase the distance at which they are visible to females. Alternatively, it has been suggested that the displays have both territorial and sexual functions (Launay & Paillat 1990), and therefore display sites may be situated at territory boundaries. The location of houbara leks relative to the locations of females has never been studied.

Most lek studies in birds are from temperate northern hemisphere regions on species with classical leks (e.g., ruffs *Philomachus pugnax*, sage grouse, *Centrocercus urophasianus*). One reason that a detailed understanding of lekking behaviour is unknown for houbara is that the birds are difficult to catch, mark and observe (Seddon *et al.*, 1999, Maloney 2001), and these difficulties are common to studies of many members of the bustard group (see del Hoyo *et al.*, 1996). However, species such as houbara, which have dispersed leks and are found in open desert areas, and have pan-African origins (c.f., Hoglund & Alatalo 1995), offer an opportunity to examine lek formation under a suite of different phylogenetic, environmental and behavioural evolutionary pressures.

Not all of the three hypotheses on lek formation described above can be easily tested for houbara, because the cryptic behaviour of the species limits the ability of workers to collect appropriate and comprehensive data. Hotshot and female preference models are the most difficult to test. The hotshot model requires detailed knowledge of the interception and mating rates of female houbara by satellite males. Direct observation of copulation is extremely rare (Gaucher *et al.*, 1996, Chapter 7) and while use of micro-satellite DNA techniques on offspring may be a useful method of determining mating outcomes (e.g.,

Alatalo *et al.*, 1996), relative rates of mating for inferior and superior males would be difficult to determine. Similarly, female preference models require observations of individual female behaviour (e.g., search times, comparisons of males, degree of harassment by males) at a level of detail that has never been previously achieved for the species. However, testing the predictions of the hotspot model are easier, because these are based on relative movements and home range utilisation of males and females that can be measured indirectly using radio-telemetry, with less emphasis on direct observation of behaviours and interactions.

Here, I test predictions of the hotspot model using a population of individually radio-tagged houbara of known age and sex that have been re-established into a 2250 km² semi-arid desert reserve in west-central Saudi Arabia. Of four components of the hotspot model commonly tested, I examine three: that males cluster where females spend the most time, where female density is greatest, or where female home ranges overlap the most. The fourth component: that males cluster along routes commonly used by females moving between sites, was not tested because it was not possible to determine where such routes lay. Specifically, I predict that male houbara display sites are clustered either: (1) at the core home range sites of females, (2) at sites where numbers of females are greatest or, (3) at sites where the most females have overlapping home ranges.

Methods

Are display sites located where females spend most time?

I radio-tracked male and female houbara over three years and regularly determined their locations (see Chapter 4, 5 and 6). I used location densities as an estimate of time spent at each core site. Because sampling was regular, then the number of locations at a site directly correlates with the time the female spent at those sites. Core sites were areas of highest trajectory density determined using Hierarchical Incremental Cluster Analysis (HIC, Kenward 1987). I used cluster analyses rather than polygon methods because HIC is the preferred technique for identifying areas of maximum trajectory density (Robertson *et al.*, 1998, see Chapter 6). I selected 70 % isopleths for HIC analyses. Isopleths over 80 % were

more likely to contain outlying points that greatly inflated home range core areas. Only data from breeding seasons (defined as January-April, Chapter 6) in three years (1996 – 1998) were included. Comparative HIC analysis is sensitive to differences in sample size (Boulanger & White 1990, Aebischer *et al.*, 1993, Swihart & Slade 1997, Robertson *et al.*, 1998). I therefore set N at 18 locations per breeding season (i.e., one sample per 6.7 days). To achieve this, I sub-sampled larger data sets in a stratified random manner to include data from every week period within the season. Individuals from which fewer than 18 locations in a season were available were excluded from that season's data.

I then plotted female HIC core ranges, and overlaid the sites where males displayed. The number of occasions when female home ranges and male display sites corresponded (i.e., where males were displaying within a female's core range) were tallied per year and compared with the number of female core ranges that did not contain display sites. Because HIC analysis often produced multiple cores, and because males sometimes displayed at two different sites within a season, I recorded overlaps once per male, for any one of a female's core ranges with any one of a male's display sites. Therefore, display sites and home ranges per individual were considered either overlapping, or not overlapping, regardless of the number of sites at which the two individuals may have encountered each other. The observed proportion of overlapping and non-overlapping groups was compared to expected values using a Chi-square Goodness of Fit test. If males were displaying at sites where females spent the most time, then most males were predicted to display in female core ranges. Therefore, I extrinsically set expected values to a level where 75 % of male display sites would overlap with female core home ranges (Sokal & Rohlf 1981, p.700).

Are display sites located where female densities are highest?

Female home ranges were large, but females were not regularly distributed over the reserve (Chapter 6). Deciding which females should be included in a sub-population to determine female density at each display site is problematic, and depends entirely on scale. For example, should all females in the reserve be considered one population because all are capable of flights of hundreds of kms, and therefore all male display sites could be sampled? Or should only females that were known to occur at or near the display site itself be included *a posteriori*?

To determine female densities I calculated population size on a grid cell basis (White & Garrott 1990, Mizutani & Jewell 1998), because this generated an array of estimates of female density for the entire reserve over which display sites could be plotted. I used an unbiased estimate of grid cell size based on known characteristics of male displays and female home ranges. Running displays of males ranged over 1 – 2 km, and several males may display in adjacent sites (Chapter 7). Thus, for several males to have display sites in the same general site within the reserve (i.e., a dispersed lek) an area of tens of km² is required. A grid scale at this magnitude is appropriate for females as well. In the breeding season female home ranges overlapped and averaged 14.8 km² (~4 x 4 km) in area (70 % BNE, Chapter 6). Therefore, I conservatively chose a grid cell size of 5 x 5 km (25 km²) as the grid cell unit in which to count the number of females.

I plotted all data points per female, used these points to record the presence or absence of each female in each cell. A female was recorded in a grid cell if one or more locations fell within the grid boundary. Grid cell position was arbitrarily based on 5 km increments of UTM co-ordinates (White & Garrott 1990) starting at X, Y = (130, 2430), and moving north and east. All grid cells partially or fully within the Mahazat as-Sayd Reserve boundary fence were included. Thus, there were 124 total cells covering 3100 km² of the reserve and its immediate surroundings. Display sites were predicted to occur in grid cells that have the highest number of female locations more often than grid cells with few females. I used Chi-square analyses to determine whether the observed number of display sites was higher in cells with higher female densities than was expected.

Are display sites located where most female home ranges overlap?

Range overlap is a difficult measure to determine, because regardless of the method used, outlines drawn around a sample of locations rarely describe the true utilisation of an area by an animal (e.g., see White & Garrott 1990, Robertson *et al.*, 1998). Most polygon methods for describing home ranges are unstable, and depending on the sample of locations analysed, range size and shape will differ dramatically (Robertson *et al.*, 1998). For most range estimators there is a trade-off between location density and range stability, and there is no single best approach. Bivariate Normal Ellipses (BNE, Jennrich & Turner 1969, see Chapter 6) are the most stable of several common methods used to determine range size (Robertson *et al.*, 1998), therefore they are best for comparisons among females and years.

I used the 70 % Bivariate Normal Ellipse (BNE) home range estimates for females in each of three breeding seasons as described in Chapter 6. For each year separately, I plotted these ranges, and overlaid the display locations of males. I recorded the number of female home ranges that overlapped each display site, and compared the proportion of display sites that were encompassed by different numbers of overlapping female ranges with the proportion of overlapping home ranges available using a Chi-square test. The expected distribution of potential display sites was determined by plotting female home ranges, examining the resulting areas of home range overlap, and recording the number of sites where 2, 3, 4, or 5 females had over-lapping home ranges.

Houbara included in the analyses

All adult males that I recorded as displaying, as determined by display tracks or direct observation, and that were greater than one year old were included (Table 8.1). I defined a lek as two or males displaying within 2 km of each other within the same season, and I included males at leks, and those that displayed in isolation of other males. I excluded one-year-old males because they perform partial displays on rare occasions, they do not have fully developed display feathers, and some one-year-old males were never seen displaying despite regular attempts to record this. There was one adult male present in the reserve during the study for which I could not locate a specific display site. This male (tx5260, Table 8.1) was located in the north eastern region of the reserve, which was mostly open, flat, gravel plains with scattered vegetation patches. I could not locate an observation point to watch this male, and was unable to detect display tracks on the hard gravel. From the erratic radio signals and the presence of filamentous display feathers on this male, I considered that he was displaying regularly in an area of approximately 1 km². I included an estimated display location at the place where this male was most frequently found early in the morning during the 1997 and 1998 breeding seasons. All adult females one year of age and older were included, because one-year-old females were capable of breeding (Gélinaud *et al.*, 1997, Chapter 4, Table 8.1).

Table 8.1: Ring and transmitter (tx) frequencies, and the age and years of inclusion for each adult houbara in Mahazat as-Sayd Reserve, by sex. ✓ indicates that the bird was included in the analyses for that year.

Permanent ring number	Tx code	1996	Age in 1996	1997	Age in 1997	1998	Age in 1998
155	4033	✓	3	✓	4	✓	5
288	4060	-	-	-	1	✓	2
270	4282	-	-	-	1	✓	2
685	4933	-	-	-	-	-	1
228	5123	✓	2	-	-	-	-
557	5124	-	-	-	1	✓	2
224	5177	✓	2	✓	3	✓	4
263	5194	-	1	*	2	✓	3
248	5260	-	1	✓**	2	✓**	3
238	5282	✓	2	✓	3	✓	4
691	5385	-	-	-	-	-	1
160	5411	✓	3	✓	4	✓	5
161	5540	✓	2	✓	3	✓	4
211	5547	✓	2	✓	3	✓	4
214	5653	✓	2	✓	3	✓	4
239	5674	✓	2	✓	3	✓	4
233	5707	✓	2	✓	3	✓	4
Total males		10		10		14	
259	4395	✓	1	✓	2	✓	3
292	4412	-	-	✓	1	✓	2
170	5026	✓	3	✓	4	✓	5
167	5113	✓	2	✓	3	✓	4
153	5131	✓	3	✓	4	-	-
523	5210	✓	2	✓	3	✓	4
186	5240	✓	3	✓	4	✓	5
171	5268	✓	4	✓	5	-	-
240	5358	✓	2	✓	3	✓	4
182	5419	✓	3	✓	4	✓	5
191	5441	✓	3	✓	4	✓	5
220	5496	✓	2	✓	3	✓	4
542	5515	✓	1	✓	2	✓	3
216	5590	✓	1	✓	2	✓	3
524	5598	✓	2	✓	3	✓	4
Total females		14		15		13	

* erratic transmitter prevented location in this season

** an estimated display location included for this male in these years

Results

Are displays at sites where females spend most time?

Display sites of males were not situated at the sites where females spent most of their time, and this result was highly significant ($\chi^2 = 71.7$, D.F. = 1, $P < 0.001$). In total, over the three years, only five (14 %) of 36 male display sites overlapped with female 70 % HIC core home ranges (Fig. 8.1).

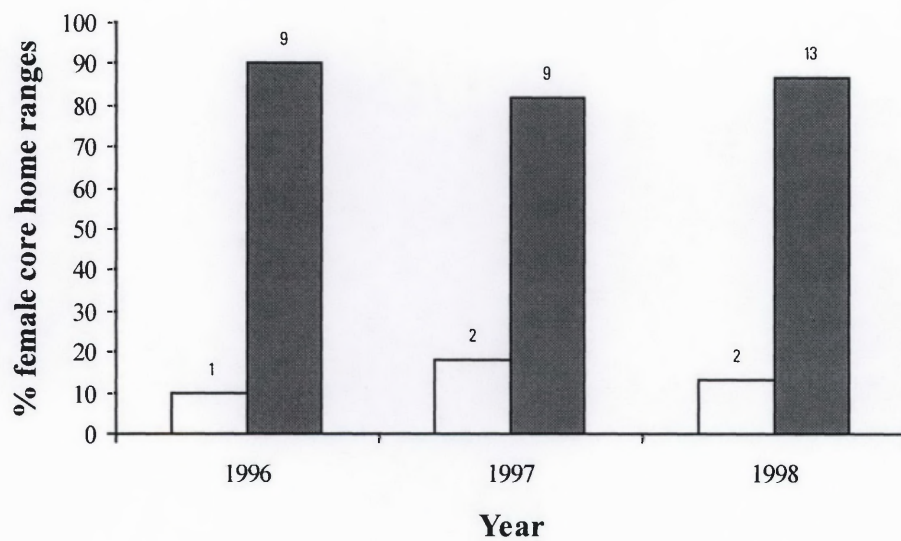


Figure 8.1: Percent of female core home ranges (70 % HIC) that encompassed (open bars), or excluded (shaded bars) one or more male display sites in each of three spring seasons from 1996 to 1998. Numbers above bars are the number of male display sites. N females = 10 in 1996, 11 in 1997, 15 in 1998.

Most display sites were located in the southern quarter of the reserve, but in contrast, female home ranges were widespread across the reserve. No males were present near female home ranges in the western or north western areas of the reserve in any year, nor were any adult males present in the north eastern areas of the reserve in 1996, even though many females spent most of their time there. Two males were found in north eastern sites in 1997, one (tx5707) moved from the south, and the other (tx5260) reached adult age in 1997, but there were no leks in the east or the west, despite the presence of females in these regions (Fig. 8.2).

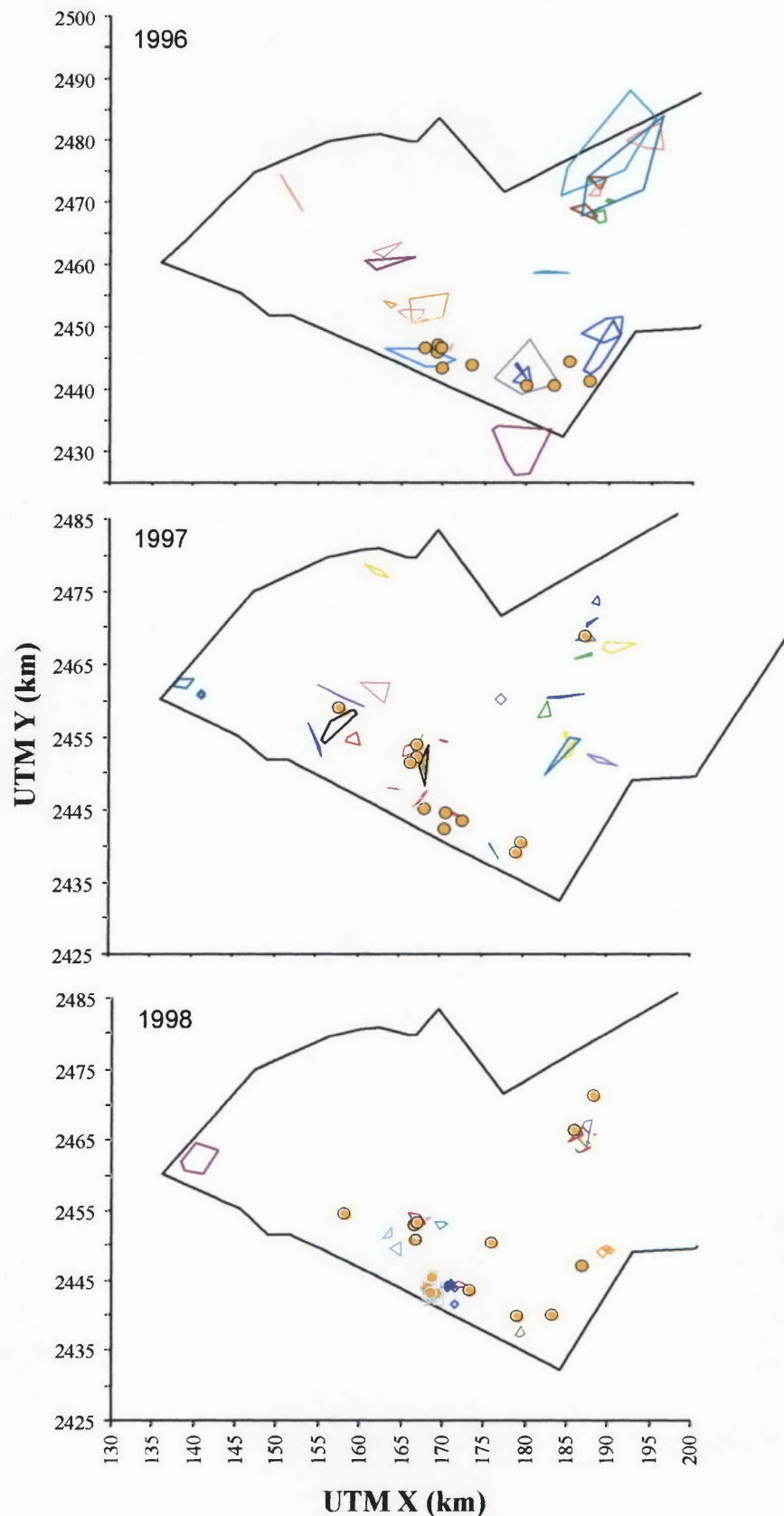


Figure 8.2: Location of cores of female home ranges (70 % HIC polygons) and male display sites (orange circles) in Mahazat as-Sayd Reserve in each of three spring seasons from 1996 to 1998. Estimated sites for male tx5260 are included, see methods for further details. UTM co-ordinates as per Fig. 3.3. Note Y-axis scale differs in 1996.

Young males did not reliably seek out sites with many females. In 1997, only one young male began displaying, and its display was near a cluster of females to the centre-west of the reserve. However, in 1998, four young males began displaying; two were more than 5 km from the nearest female core range, one was 3 km, and the remaining male displayed in the southern region where many older males had display arenas. Two males (txs: 5177, 5653) had display sites in the south of the reserve that were near to female cores in 1996. However, these males continued to display in the same area in 1997 and 1998, despite the paucity of females nearby.

Are display sites located where female densities are highest?

Display sites were significantly more likely to be located in areas of the reserve where female density was high (all years combined, $\chi^2 = 81.6$, D.F. = 3, $P < 0.0001$, Fig. 8.3). In each year, proportionately more display sites were located in sites with 3 – 4 females per 25 km², compared to sites where there were more or fewer houbara.

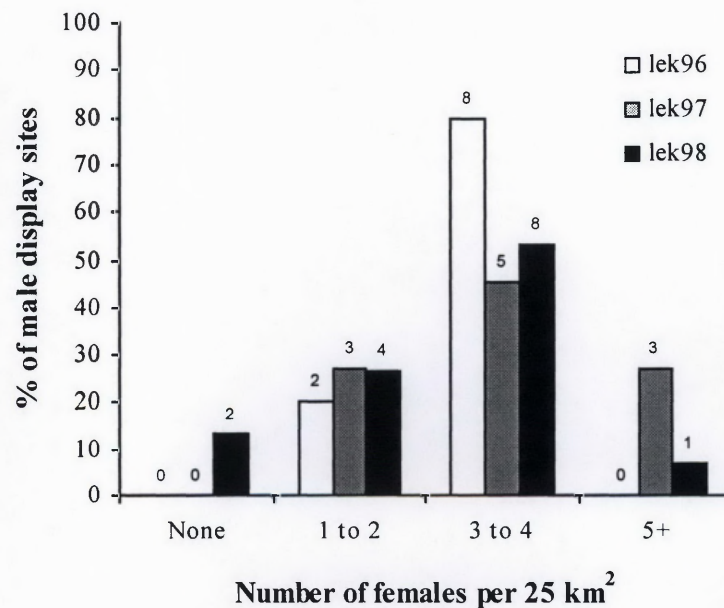


Figure 8.3: Percentage of male display sites in 25 km² grid cells for four categories of female density, for three spring seasons from 1996 to 1998. Grid cells were arbitrarily based at a start point of UTM X, Y co-ordinates 130, 2430, to the south west of the reserve (see Fig. 3.3). Number of females is the sum of the number of females recorded as present within each grid cell based on all locations during each breeding season. Numbers above bars are the number of male display sites.

Maximum female density was seven females per 25 km² in the north east of the reserve in 1996, but no males were recorded displaying in this region. Two males in 1998 displayed in grid cells where no females were recorded. Locations of females were recorded in 30 – 58 (24 – 47 %) of the 124 grid cells during the three breeding seasons from 1996 to 1998. Male display sites were clustered, and occurred in only 6 – 10 squares during the same period.

Do males display at sites where most female home ranges overlap?

On average, each display site was encompassed by 1.48 ± 0.41 (mean \pm 95 % C.I.) female home ranges. Eleven (31 %) of the 36 male display sites used in the reserve over the three seasons were not located inside a female home range, and some were up to 8 km from the nearest female's home range boundary (Fig. 8.4). Of the remaining 25 display sites that were encompassed by female home ranges, 14 were included within one female's home range, three within two, two within three, five within four, and one within five females' ranges (Fig. 8.5). Overall, one quarter (24 %) of male display sites were located at sites where four or five females had overlapping home ranges (i.e. hotspots), even though these hotspots comprised only 11 % of 122 (43 no overlap, 79 where 2-5 female home ranges overlap) locations available. In contrast, fewer males than expected had display sites at locations where two or three female home ranges overlapped. Differences in observed locations of male display sites and available sites of female home range overlap were significant (all years combined, $\chi^2 = 9.62$, D.F. = 4, P = 0.047, Fig. 8.5).

Females were variable in their home range locations with respect to male display sites. One female's home range encompassed eight display sites, but more commonly, 49 % of female home ranges did not encompass display sites. On average, female home ranges encompassed 1.32 ± 0.49 (mean \pm 95 % C.I.) display sites. Many females had home ranges that were more than 5 km from the nearest display site: seven of nine females in 1996 were in the north east, east, and west of the reserve, and one female in 1997 and two in 1998 were in the east of the reserve (Fig. 8.4).

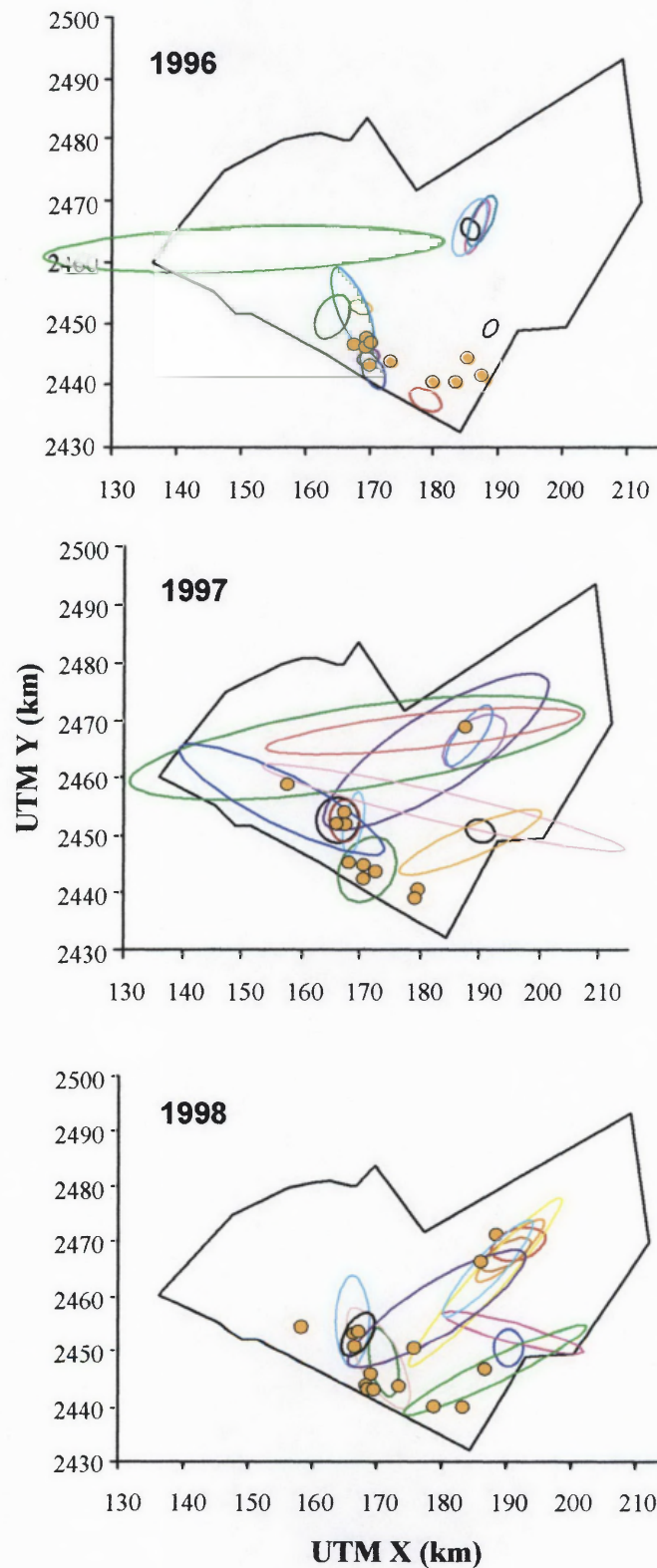


Figure 8.4: Location of female home ranges (70 % BNE) showing regions of overlap, and male display sites (orange circles) in Mahazat as-Sayd Reserve in each of three breeding seasons from 1996 to 1998. UTM co-ordinates as per Fig. 3.3.

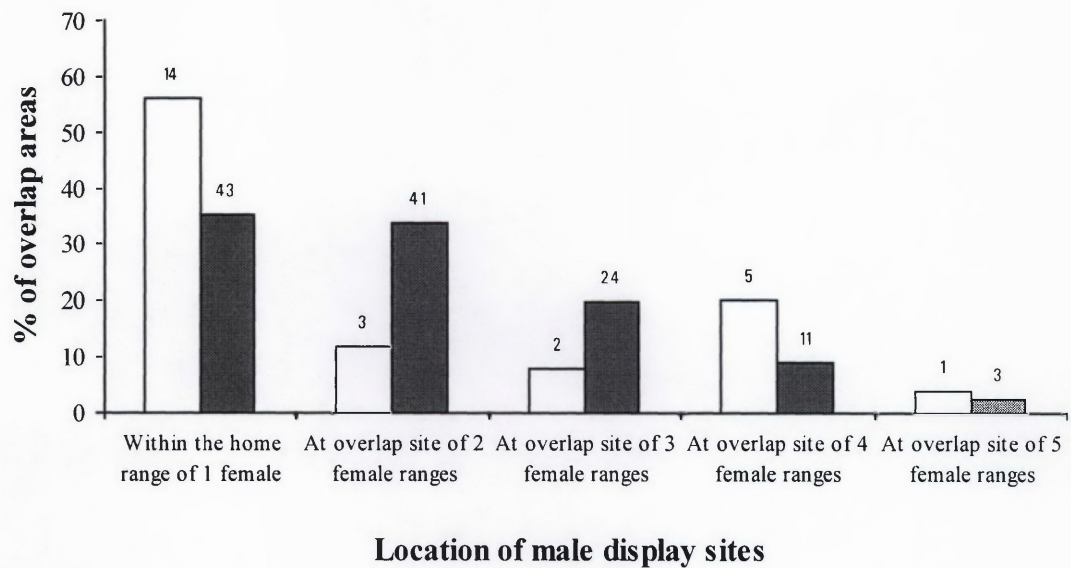


Figure 8.5: Observed location of male display sites (white bars) at regions of differing female home range overlap, compared with the availability of overlapping sites (shaded bars). N values are given above bars. For example, three male display sites were sited in the region where the home ranges of two females overlapped, yet there were 41 sites available where the home ranges of two females overlapped.

Discussion

These results show that male houbara display sites in Mahazat as-Sayd Reserve are not located randomly with respect to females. Males were more likely to display in places where female densities were higher, and in sites where many female home ranges overlapped. The behavioural or ecological mechanisms determining this relationship are not clear. Possibly, either sex may be selecting display sites or home ranges based on the location of the other sex. However, I suggest that it is the males that select display sites based on hotspots of female home range overlap, i.e., at locations where males are most likely to encounter many females. The alternative, that females are selecting and utilising ranges near to male display sites, was not supported in this study: female core ranges were not located at display sites.

For houbara males, this strategy seems sensible for two reasons. First, locating a display site within a female's home range may actually be very difficult to achieve consistently. Female houbara movements in Mahazat as-Sayd Reserve fit a pattern consistent with their changing use of small localised patches, while still maintaining general site fidelity to a larger area (Chapter 6). Males are unlikely to be able to predict the location of core female home ranges in advance, because food is temporally and spatially patchy within the reserve (Combreau & Smith 1997), and in desert environments in general (Rotenberry & Wiens 1980, Louw 1984). Patchy environmental conditions occur because annual rainfall is unevenly distributed in the region (see Appendix 1), and this is further exacerbated by disjunct vegetation patterns, and by uneven run-off and accumulation of rain in temporary water channels. Patches are small, often only a few hundred hectares in area, thus habitat variation is large on smaller scales (up to a few kms). Second, locating a display site within the core range of a single female may limit overall male mating success, because at these core sites males may be excluded from gaining access to other females. In the breeding season females are relatively solitary, and do not associate with other females. Female home ranges are discreet and there is little female – female home range overlap (Chapter 6), possibly because females actively defend breeding territories against other females. Further, females may actively exclude males from core home range areas when breeding, preventing males from displaying in these areas. My observations of single females raising offspring without the support of males (Chapter 4) supports an hypothesis of exclusivity of females' core home range areas.

Houbara males have two options when locating their display sites on the periphery of female ranges. Either they can locate a female, set up a temporary display site, display, mate with her then move to a new site and new female (i.e., be "floaters"), or they can chose a single display site and use it for the duration of the breeding season (i.e., be "court-holders"). Floaters are predicted to have many temporary display sites on the edges of many female ranges, whereas court-holders will have one site in an area with many females. In this population, males have fixed display sites that rarely vary over the course of the breeding season or over several seasons (Chapter 7), and therefore, I suggest that houbara are court-holders, with little evidence of a floating male population.

In contrast, on classical leks, both resident and satellite males are frequently recorded (e.g., Hugie & Lank 1997), and while there are few reported studies of male behaviour in bird

species with dispersed leks, most have found that both floater and court-holder strategies occur. For example, Westcott (1993) and Westcott & Smith (1994) found that there were three categories of males in Ochre-bellied flycatchers (*Mionectes oleagineus*): territorial males, satellites, and floaters. In total, 48 % of male flycatchers were floaters and did not have a display territory, and territory holders were using different habitat types from floater males. Similarly, male buff-breasted sandpipers (*Tryngites subruficollis*) display on leks or solitarily, and leave leks when female numbers decline, in favour of solitary display sites in other locations (Lanctot & Weatherhead 1997). Floaters may be absent or selected against in some populations because they are inferior to court-holding males, and are therefore unlikely to be able to compete for space or females at leks. For example, court-holding Jackson's widowbirds (*Euplectes jacksoni*) had larger bodies, wings, collars, and tails than floaters (Andersson 1993). Floaters may even be males that are waiting in turn to take over prime territories (Zack & Stutchbury 1992).

Possibly, the absence of floaters in this study is because the population is not yet at carrying capacity, and therefore all males are able to find suitable display sites. Certainly, habitat for houbara display sites is not limiting in Mahazat as-Sayd Reserve: there were many unused but potential display sites that were similar to those used by displaying males (Fig. 8.6). While I found no evidence of floater houbara males, a floater-type strategy would appear to be a favourable option if males were to maximise their reproductive potential in a similar manner to buff-breasted sandpipers. Females in Mahazat as-Sayd Reserve are widely dispersed, and have limited ranges, which exclude large areas of the reserve. Therefore, for a male to gain access to many females, the best strategy should have been to travel to several distinct sites throughout the reserve in order to maximise female encounters. Instead, males generally remained on the same display site for the entire season, and for some males, this behaviour occurred even when they had access to none, or only a few females. Presumably, displaying in a site in the absence of females is a non-adaptive strategy that will not persist in this population. I conclude then, that males are encouraged to be court-holders because this strategy is rewarded by more visits from more females on average, than an alternative strategy where males are floaters.

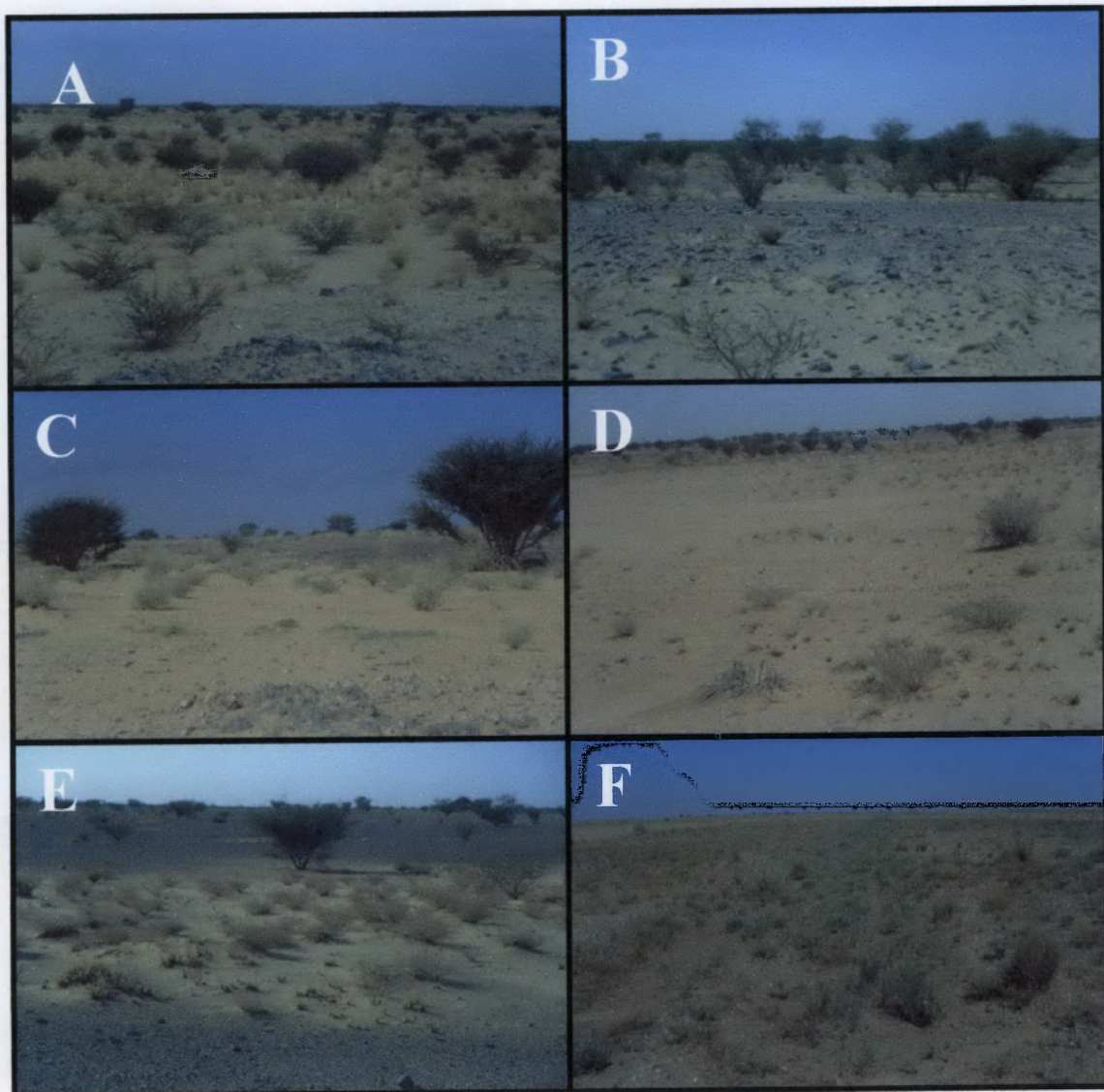


Figure 8.6: Typical display sites used by houbara males in Mahazat as-Sayd Reserve. Display sites are from: (A) tx5177 in the south east of the reserve, (B) tx5653 - south east, (C) tx5411 - south, (D) tx5674 - central, (E) tx5540 - south and, (F) tx5707 - north east.

Male houbara had a large number of sites to choose from where female home ranges overlapped; yet they were mostly clustered around one site in the southern section of the reserve. Clustering in groups may further enhance the total number of female visits to court-holding males because females have to travel to fewer sites to find males, they may be more able to detect males displaying in groups, and they may learn through experience where to locate large numbers of males (Hoglund & Alatalo 1995). The use of lek sites has other benefits to males in that it reduces male aggression and increases their ability to learn about other males (Widemo 1997). Future study should focus on determining female visitation rates to male display sites, using continuous automated recording at all display sites, including at night, to show that female visiting rates are higher at display sites that have more males, and therefore that houbara males benefit from a court-holders strategy. Further, if it is beneficial for males to cluster, then young males should settle close to other males, and not at new sites near to females. The few young males observed displaying in 1998 in this study displayed near to males in the south of the reserve, and not, for example, near to the isolated females in the west or north east of the reserve.

Models of lek formation

My results clearly support some predictions of the hotspot model of lek formation. Male display sites occurred in regions where female densities were high, and where home ranges of females had a high degree of overlap. One prediction, that males cluster at sites where females spend most of their time was not supported. A fourth prediction of the hotspot model, that leks form along female travel routes (e.g., Bradbury 1981, Gibson 1996, Westcott 1997) could not be tested, because female travel routes were unknown. However, I suggest that lek sites are unlikely to occur on travel routes of female houbara, for three reasons. First, habitat in the reserve is patchy in all directions, with no geographical barriers or features, and thus females are unlikely to be travelling along defined pathways. Second, females are usually solitary, so few birds are likely to be travelling to and from the same locations. Third, my observations of male display sites show that they were mostly distributed along the southern boundary of the reserve (Figure 8.2), and not in localities that may be predicted to have more female movements, i.e., to the north of this site where most females lived.

Despite criticism that hotspot models can only describe coarse levels of male distribution and that other models are needed to describe the finer scale of lek formation (e.g., Balmford *et al.*, 1993), subsequent studies have found that predictions of the hotspot model are supported in a wide range of species: in greater prairie chickens (*Tympanuchus cupido*, Schroeder & White 1993), in sage grouse (*Centrocercus urophasianus*, Gibson 1996), in Hawaiian fruit fly (*Drosophila grimshai*, Droney 1994), and in Ochre-bellied flycatchers (Westcott 1997). However, some studies have failed to find evidence supporting hotspot predictions (e.g., Balmford *et al.*, 1993, Wickman *et al.*, 1995, Wikelski *et al.*, 1996), and have suggested that alternative female preference or hotshot models were more appropriate. I did not attempt to test the relative importance of either female preference or hotshot males in the formation of the distribution of display sites used by houbara. However, some predictions of these models clearly do not fit patterns of houbara movements and behaviour.

In particular, I suggest that harassment-based female preference models (Clutton-Brock *et al.*, 1993) are unlikely to explain lek formation in houbara, because houbara have widely dispersed display sites at which males rarely interact, and because females do not aggregate at leks in defendable harems (see McComb & Clutton-Brock 1994). It is unclear whether hotshot males may occur in the reserve. Many of the males were young, and therefore may have still been gaining experience or reputations required to be a hotshot. At one site, five males formed a dispersed lek, and one or more of these males may have been hotshots. However, none of the other 5 – 8 males in the reserve was attracted to this site, indicating that males were not all clustering around a single superior male. Nor were males clustered around kin: in white-bearded manakins (*Manacus manacus*, Shorey *et al.*, 2000) males clustered around closely related kin, suggesting kin selection was an important in the formation of male aggregates. In this study, males were not closely related with only two males possibly having the same parents (unpubl. data, paternity in captivity sometimes uncertain because of multiple inseminations). Males did appear to differ in their ability to display over long periods (Mukhina 1993, Chapter 7), perhaps indicating that running displays of houbara offer some degree of truth-in-advertising that allow females to choose among them. Further work to test these hypotheses, that focuses on the characteristics of male displays that may indicate fitness (see e.g., Petrie & Halliday 1994, Tsuji *et al.*, 1994), and genetic determination of sires of offspring, may help determine their relative importance.

9. General discussion

In this study, I have reported on the release, survival, breeding, movements and lek formation of houbara in Mahazat as-Sayd Reserve, Saudi Arabia. I have shown that those birds that survive the release phase go on to be vigorous nesting females or displaying males, producing an average of one fledgling per female over the three study years. With only two adult deaths recorded over the same period, it is very likely that this population will be able to sustain itself in the near future. Population simulations based on 1998 breeding data show that even without continued supplementation the intrinsic growth rate (r) will be 0.091. This rate will lead to sustained growth up to an arbitrary carrying capacity of 500 birds, with no risk of extinction for all 100 simulations of 100 populations modelled (see Appendix 7 for Vortex 5.1 (Lacy 1993) population simulation parameters used). While such modelling is useful as an indicator of likely outcomes, and may determine future release strategies into the reserve, these models currently rely on several assumptions for houbara that need further testing. In particular, there are no data on recruitment rates, or the proportion of males that breed, and inter-annual variation in all of the survival and breeding parameters are largely unknown. Therefore, I recommend that researchers focus on quantifying these aspects of houbara breeding as soon as possible, to better determine whether further supplementation is required for the sustainability of this population within Mahazat as-Sayd Reserve.

Although, the reintroduction of houbara into this reserve has resulted in the establishment of a population of breeding houbara, the process has been slow. This is mainly because half of all released houbara died within 39 days of release, and within 0.9 km of the release site, and only 27 % survived to breeding age. Greater efficacy is required during the release phase to maximise initial survival rates, and thereby maximise the return from the investment conservation managers have made in this project. This in turn will enable the production of young houbara from captive facilities to be used sooner at other release sites for the establishment of other new populations, and will also make the releases more economical and effective. Increasing post-release survival will require further experimentation, and a better understanding of the cause of loss. Three factors are implicated in houbara deaths post-release: predators, food, and extreme heat. Predators (mainly foxes) killed most houbara during the release phase, usually on the first full-moon period following the houbara's movement into the reserve. Aggressively training houbara about foxes before release

increased their probability of survival after release (van Heezik *et al.*, 1999), indicating that in the absence of foxes more released houbara would survive. However, trapping and translocating foxes and feral cats did not improve the survival rates of released houbara in the long-term (Chapter 3), despite a demonstrated improvement following the first year of trapping (Combreau & Smith 1998). I hypothesised that translocated predators were returning to the release site and remaining there as a cage-trap-shy population (i.e., were cryptic predators). I proved the existence of these cryptic predators by using a different trapping method to catch several foxes that had been caught previously. I therefore tested a portable cage design to release houbara into other sites in the reserve, where foxes were less likely to be trap-shy, to avoid this problem in the future. Houbara were successfully held in portable cages at three new sites in the reserve in 1997, but following their release, all of these houbara died, and their deaths followed a similar timing and distance from release site to those released from the permanent enclosure. I concluded that cage trapping and translocation of foxes were not effective in preventing houbara mortality after release. I recommend that forms of predator control that are more aggressive, or releases of houbara into sites with few predators, need to be considered if post-survival rates are to improve significantly. In the future, once a resident population is firmly established in Mahazat as-Sayd Reserve, adult and young houbara could be caught and released into new sites as a wild-to-wild translocation. These translocated birds may have a better chance of survival because they have already been exposed to wild conditions.

Despite overwhelming evidence that predators were responsible for most deaths, I consider that released houbara have difficulty in adjusting to their post-release environment, particularly in obtaining food and avoiding water stress in extreme heat. It is likely that for many of the deaths I attributed to predators, predation was a secondary event for houbara that were too weak to avoid them. Notably, I showed that more than 10 % of birds died in a mammal-free enclosure, prior to encountering predators, and at least three released birds showed signs of death by starvation. Most releases occurred from May to July, the hottest and driest months in the reserve. Although, I was unable to show that releases from August to November resulted in higher survival rates, sample sizes were low, with only 24 houbara being released during this period. I suggest that releases have a greater chance of success when conditions in the reserve are more favourable, such as after rain or when temperatures are cooler. Relatively wet and cool conditions regularly occur from October to December. I

suggest that future research examines whether provision of supplementary food after release improves survival rate, and second, whether survival rates are improved by delaying releases until after October. Current soft-cages are small and round (Combreau & Smith 1998). If houbara are to be held at the release site for several months (from May to October), then I recommend that an improved cage design, which allows for greater movement of houbara within the cage should be used: cages that are at least 10 m long by 4 – 5 m wide by 3 – 4 m tall should be trialed.

The goal of this reintroduction project was to establish a self-sustaining population of houbara in Mahazat as-Sayd Reserve, within the context of a wider goal to protect and recover houbara populations nation-wide (Saint Jalme *et al.*, 1996b). The results of the releases and the release research reported here show that the first part of this goal is now within reach. However, in this thesis, I have demonstrated that the value of undertaking releases and closely monitoring outcomes is much wider than just achieving self-sustaining populations (and see Saint Jalme *et al.*, 1996b, Seddon *et al.*, 1995). Using these birds as experimental subjects, I have been able to provide detailed data on breeding success, breeding ecology, nest site characteristics, male display behaviour, home range and movements, and importantly, some insights into the behavioural relationships between male and female houbara that has not been achieved in detail with any other population. I have also shown that released houbara in Mahazat as-Sayd Reserve have similar breeding ecology as that reported from wild populations (see Table 4.12) that make these data relevant to other populations: with the caveat that very little is actually known about wild breeding birds on which to base captive-reared versus wild-reared comparisons. In the absence of data from wild populations, using released birds to determine aspects of ecology and behaviour is crucial for a species that is so poorly understood throughout its range.

Importantly, detailed studies of mating behaviour are required. There has been considerable speculation about the type of breeding system used by houbara, and monogamous (Cramp & Simmons 1980, and references therein), polygamous and promiscuous (Collins 1984 (for *C. u. fuertaventurae*, Launay & Paillat 1990, Launay & Loughland 1995) breeding systems have been suggested. In Mahazat as-Sayd Reserve, I was able to monitor closely all known males and females over three breeding seasons. I found no evidence of monogamous pair bonds being formed for any of the egg, chick, and fledgling rearing periods. I never observed

males incubating or even near nest sites, and males were never recorded with females that had chicks (in contrast to Gelinaud *et al.*, 1997, Combreau *et al.*, 2000). Throughout the breeding season (January to May) males ranged close to display sites, and were not recorded away from these sites. Although male and female associations were more common during breeding, these were associations during female movements to male lek sites (presumably for the purpose of mating) and not male movements to female nest sites. Therefore, I conclude that houbara in this population are polygamous breeders that have dispersed leks. Further evidence of mating success rates for different males are required to prove that one male has multiple mates, and collection of feather samples from adults and offspring for use in DNA testing would confirm this. From a theoretical viewpoint, this type of lekking system contrasts well with many other northern temperate lekking species (see Hoglund & Alatalo 1995), and offers opportunities to test mate selection theory on a new species with African origins, in a different environment (and see Chapter 8). Similarly, further study of this population as it collectively grows and gains experience, will provide an ideal setting for researchers to study the social behaviour and ecology of this species, using known individuals with a known history, and compare and contrast this population with other populations of houbara, and with other bustards.